LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF *TRUPANEA WHEELERI* CURRAN (DIPTERA: TEPHRITIDAE) ON ASTERACEAE IN SOUTHERN CALIFORNIA

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Abstract.—*Trupanea wheeleri* Curran is a multivoltine, florivorous fruit fly (Diptera: Tephritidae) infesting flower heads of a wide variety of Asteraceae in California and the western half of the United States. Four new host-plant genera and five new species records are reported. To date, *T. Wheeleri* is known from seven tribes, 15 subtribes, 28 genera, and 47 species of hosts. The egg, first through third instar larvae, and puparium are described and figured for the first time. The egg pedicel has one or two rows of aeropyles. The interspiracular processes of the first instar are large, broad, and multibranched. The anterior thoracic spiracles of the second instar each bear 7–8 papillae, more than any previously studied congeneric species. The lateral spiracular complexes of the third instar are identical to that of *T. imperfecta* (Coquillett), which is the first report of two species of *Trupanea* that share the same type and number of sensilla in their metathoracic and abdominal, lateral spiracular complexes. The life cycle of *T. wheeleri* in southern California is of the aggregative type. The eggs are inserted alongside or into the corollas of florets and ovules upon which the first instars feed in closed, preblossom flower heads. Second instars feed mainly on ovules and florets of preblossom flower heads and soft achenes of open flower heads; whereas, third instars feed on soft achenes in open and postblossom flower heads. Pupariation occurs inside the mature flower heads, from which the adults emerge about the time that the achenes are shed. Several generations are produced on a variety of hosts during the spring, summer, and fall, and overwintering is as long-lived adults. Seven species of chalcidoid Hymenoptera were reared from individual puparia and mature flower heads bearing puparia of *T. wheeleri* as solitary, primary, larval-pupal endoparasitoids: *Eurytoma* n. sp.? (Eurytomidae), *Eurytoma obtusiventris* Gahan (Eurytomidae), *Eurytoma veronia* Bugbee (Eurytomidae), *Eupelmus* sp. (Eupelmidae), *Mesopolobus* sp. (Pteromalidae), *Pteromalus* sp. (Pteromalidae), *Torymus* sp. (Torymidae).

Key Words: Insecta, *Trupanea*, Asteraceae, nonfrugivorous Tephritidae, biology, taxonomy of immature stages and adults, flower-head feeding, host-plant range, parasitoids

This is the penultimate paper in our recent series on *Trupanea,* one of the larger and more widespread genera of nonfrugivorous fruit flies in North America and California, though of little or no economic importance (Foote and Blanc 1963, Foote et al. 1993). *Trupanea* remained little known (Foote 1960, Foote et al. 1993) until we published detailed life histories of ten species from southern California (Cavender

and Goeden 1982; Goeden 1987, 1988; Goeden and Teerink 1997b, 1998, 1999; Goeden et al. 1998a, b; Headrick and Goeden 1991; Knio et al. 1996b), along with descriptions of their immature stages (Cavender and Goeden 1982; Goeden and Teerink 1997b, 1998, 1999; Goeden et al. 1998a, b; Headrick and Goeden 1991; Knio et al. 1996a; Teerink and Goeden 1998, 1999). In this paper we describe the life history and immature stages of an eleventh species, *T. wheeleri* Curran.

MATERIALS AND METHODS

This study was based in large part on dissections of subsamples of flower heads of Asteraceae infested by *T. wheeleri* from samples collected since 1990 in southern California in the manner described by Goeden (1985, 1992). One-liter samples of excised, immature and mature flower heads containing eggs, larvae, and puparia were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Twenty-two eggs, 15 first-, 10 second-, and 12 third-instar larvae, and seven puparia dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Additional puparia were placed in separate, glass shell vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH and two, 1-h immersions in Hexamethlydisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, and studied with a Philips XL30-FEG scanning electron microscope in the Institute of Geophysics and Planetary Physics, University of California, Riverside.

Most adults reared from isolated puparia were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cages were used for longevity studies in the insectary of the Department of Entomology, University of California, Riverside, at 25 ± 1°C, and 14/10 (L/D) photoperiod. Virgin male and female flies obtained from emergence vials also were paired (n = 3) in clear-plastic petri dishes provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1991, 1994) for observations of their courtship and copulation behavior.

Plant names used in this paper follow Hickman (1993) and Bremer (1994); tephritid names and adult terminology follow Foote et al. (1993). Terminology and telegraphic format used to describe the immature stages follow Goeden and Teerink (1997a, b; 1998, 1999), Goeden et al. (1998a, b), Headrick and Goeden (1991), Knio et al. (1996a), Teerink and Goeden (1998, 1999), and our earlier works cited therein. Means ± SE are used throughout this paper. Voucher specimens of *T. wheeleri* and its parasitoids reside in the research collections of RDG; preserved specimens of eggs, larvae and puparia are stored in a separate collection of immature Tephritidae acquired by JAT and now maintained by RDG.

RESULTS AND DISCUSSION

Taxonomy

Adult.—*Trupanea wheeleri* was first described by Curran (1932) from a female holotype from San Diego Co., California, as *Trypanea wheeleri. Trypanea* is a misspelling of *Trupanea.* Curran (1932), Foote (1960), Foote and Blanc (1963), and Foote et al. (1993) pictured the wing pattern of the female and male, which, unlike those of several North American *Trupanea* spp., is not overtly sexually dimorphic (Foot et al. 1993). However, sex-related, wing-pattern variations were found by RDG in *T. whee-*

Table 1. Incidences (%) of absence/complete-/incompleteness of proximal and distal rays in cell dm in wings of 423 ♂ and 376 ♀ *T. wheeleri* reared from flower heads of native Asteraceae in southern California during 1989–1997.

Left wing						Right wing					
Proximal ray			Distal ray			Proximal ray			Distal ray		
M[a]	B[a]	C[a]	M	B	C	M	B	C	M	B	C
Males											
205	186	32	0	191	232	201	183	39	1	189	233
(48.5)	(44.0)	(7.5)	(0.0)	(45.2)	(54.8)	(47.5)	(43.3)	(9.2)	(0.2)	(44.7)	(55.1)
Females											
117	197	62	0	87	289	114	200	62	0	90	286
(31.1)	(52.4)	(16.5)	(0.0)	(23.1)	(76.9)	(30.3)	(53.2)	(16.5)	(0.0)	(23.9)	(76.1)

[a] M = missing, B = broken, C = complete.

leri. Foote et al. (1993, p. 446) cautioned that the ". . . identification of this species must be approached with care, as the proximal ray in cell dm varies from completely present to completely absent." RDG quantified the variation in this key character in reared specimens of *T. wheeleri* from California in his research collection (Table 1). The data in Table 1 show that the proximal ray is much more prone to be missing than complete than is the distal ray in both wings of males as well as females. In nearly half of both wings examined in males, the proximal and distal rays were broken, a condition which Foote et al. (1993, p. 446) described for the proximal ray as, ". . . the two ends of this ray are visible as outcroppings in the dark area around vein r-m and anteriorly-directed extensions of the distal end of the elongate marking on vein CuA_1." Among females, however, the proximal ray was twice as likely to be broken than the distal ray (Table 1), and unlike the proximal ray, this broken ray in both sexes usually appeared as a posteriorly-directed outcropping arising midway between cross-veins r-m and dm-cu along vein M.

Foote et al. (1993) also noted that the holotype has the proximal ray complete in one wing, but almost completely missing in the other. Indeed, in 99 (23.4%) of the 423 males and 69 (18.4%) of the 376 females examined (Table 1), the proximal and distal rays of one wing differed as to whether they were missing, broken, and complete in the other wing of the same individuals. Finally, 32 (7.6%) of all males and 17 (4.5%) of all females lacked the elongated darkening along vein CuA_1 or had this infuscation reduced, sometimes to a spot, as in some *T. actinobola* (Loew), *T. jonesi* Curran, *T. texana* Malloch, and *T. vicina* (Wulp) (Foote et al. 1993), yet all of these variants were reared along with *T. wheeleri* from the same samples of flower heads of known hosts of *T. wheeleri*. Misidentifications of such variants may explain the limited records in Foote et al. (1993) for *T. texana* from southern California, where we have not yet reared this species. This variation may also help to explain difficulties experienced in distinguishing some females of *T. actinobola* from *T. wheeleri* (Goeden et al. 1998b). In most instances, however, the infuscation along vein CuA_1 combined with the dark ray connecting the pterostigma with vein r-m that is narrower than the length of the pterostigma serve to distinguish *T. wheeleri* from all North American congeners (Foote et al. 1993).

Immature stages.—The eggs, larvae, and puparium heretofore have not been described nor illustrated.

Egg: Twenty-seven eggs of *T. wheeleri* dissected from field-collected flower heads were white, opaque, smooth, elongate-ellip-
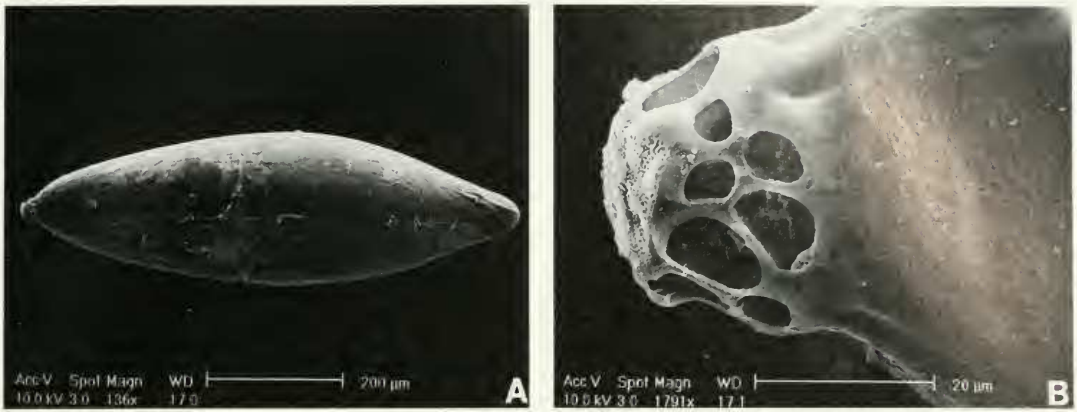
Fig. 1.   Egg of *Trupanea wheeleri:* (A) habitus, anterior end to left: (B) pedicel, aeropyles.

soidal, 0.63 ± 0.003 (range, 0.58–0.64) mm long, 0.18 ± 0.003 (range, 0.16–0.20) mm wide, smoothly rounded at tapered basal end (Fig. 1A); peg-like pedicel 0.02 mm long, with 1–2 rows of aeropyles (Fig. 1B).

The egg of *T. wheeleri* is similar to that of *T. bisetosa* in possessing one or two rows of aeropyles, all other species of *Trupanea* previously studied have only one row (Goeden and Teerink 1997b, 1998, 1999; Goeden et al. 1998a, b; Headrick and Goeden 1991; Knio et al. 1996a; Teerink and Goeden 1998, 1999). The egg of *T. bisetosa* is much longer, however, than that of *T. wheeleri* (Knio et al. 1996a). The *T. wheeleri* egg also is slightly larger than the egg of *T. pseudovicina* (Goeden and Teerink 1998a), wider than that of *T. arizonensis* (Goeden and Teerink 1998b), but smaller than that of *T. imperfecta* (Teerink and Goeden 1998).

First instar: White, elongate-cylindrical, rounded anteriorly and posteriorly (Fig. 2A), minute acanthae circumscribe intersegmental lines; gnathocephalon smooth, lacking rugose pads (Fig. 2B); dorsal sensory organ a dome-shaped papilla (Fig. 2B-1, 2C-1); anterior sensory lobe (Fig. 2B-2), bears terminal sensory organ (Fig. 2C-2), pit sensory organ (Fig. 2C-3), lateral sensory organ (Fig. 2C-4) and supralateral sensory organ (Fig. 2C-5); stomal sense organ reduced and ventrad of anterior sensory

lobe (Fig. 2B-3); mouth hook bidentate (Fig. 2B-4, 2D-1); median oral lobe laterally flattened (Fig. 2B-5, D-2); labial lobe with two pore sensilla (Fig. 2D-3); a pair of integumental petals dorsad of mouth hooks (Fig. 2B-6, 2D-4); pit sensillum laterad of mouth lumen (Fig. 2D-5); minute acanthae ventrad of mouth lumen; anterior thoracic spiracle absent; caudal segment with two stelex sensilla dorsad and ventrad of posterior spiracular plates; posterior spiracular plate bears two ovoid rimae, ca. 0.008 mm in length (Fig. 2E-1), and four interspiracular processes, each with 1–2, multi-dentate branches, longest measuring 0.007 mm (Fig. 2E-2); intermediate sensory complex with a stelex sensillum (Fig. 2F-1) and a medusoid sensillum (Fig. 2F-2).

The first instar is similar in general habitus and sensory structures to previously studied *Trupanea* species (Goeden and Teerink 1997b, 1998, 1999; Goeden et al. 1998a, b; Knio et al. 1996a; Teerink and Goeden 1998, 1999). However, the interspiracular processes are large, broad, and apically multi-branched, and thus are far more elaborate than those of, for example, *T. arizonensis* (Goeden and Teerink 1998) and *T. conjuncta* (Teerink and Goeden 1998).

Second instar: White, elongate-cylindrical, tapering anteriorly, rounded posteriorly (Fig. 3A), minute acanthae circumscribe in-
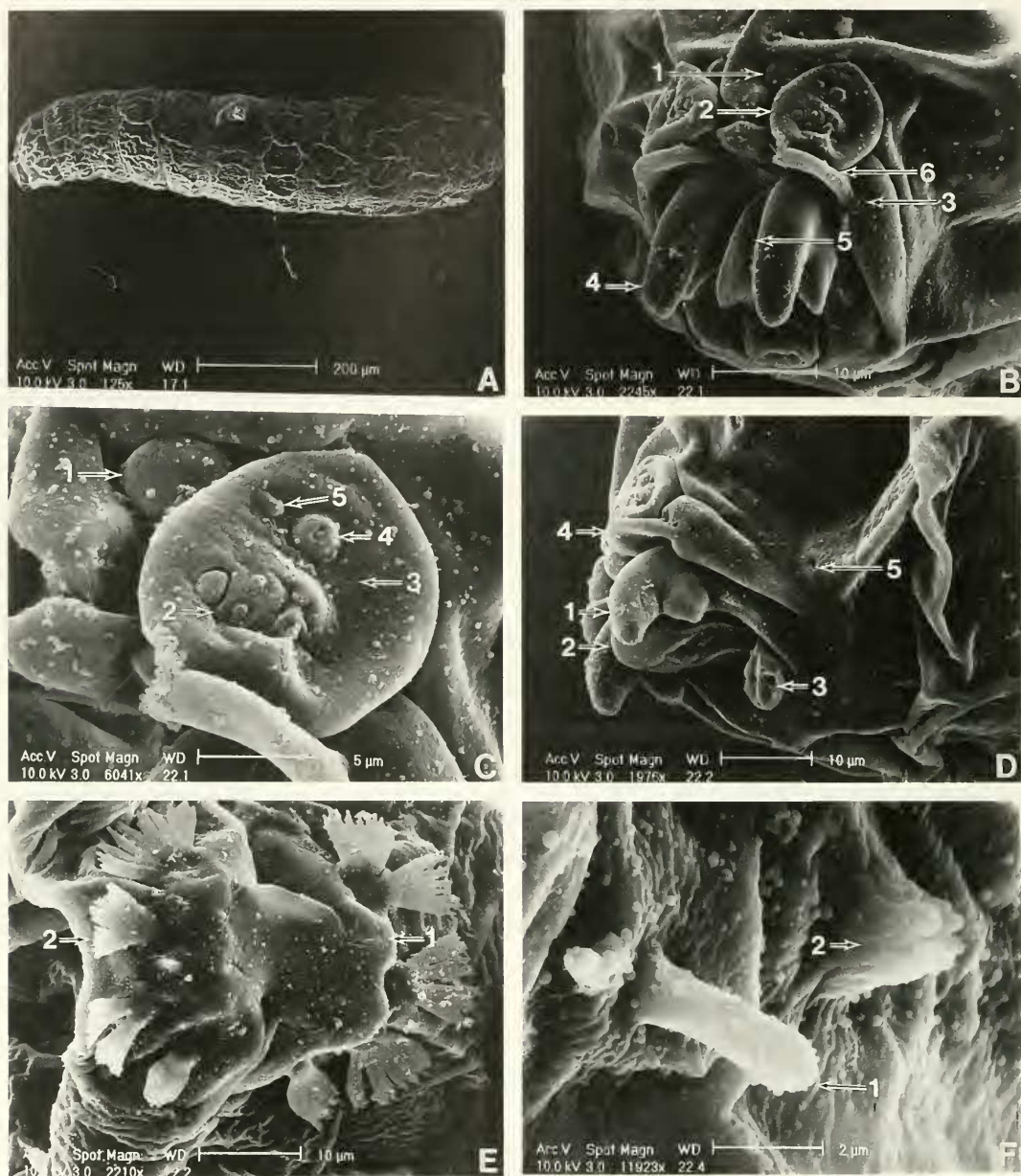
Fig. 2.   First instar of *Trupanea wheeleri:* (A) habitus, anterior end to left; (B) gnathocephalon, anterior view, 1—dorsal sensory organ, 2—anterior sensory lobe, 3—stomal sense organ, 4—mouth hook, 5—median oral lobe, 6—integumental petal; (C) anterior sensory lobe, 1—dorsal sensory organ, 2—terminal sensory organ, 3—pit sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ; (D) gnathocephalon, ventral view, 1—mouth hook, 2—median oral lobe, 3—labial lobe pore sensilla, 4—integumental petal, 5—pit sensillum; (E) posterior spiracular plates, 1—rima, 2—interspiracular process; (F) intermediate sensory complex, 1—stelex sensillum, 2—medusoid sensillum.
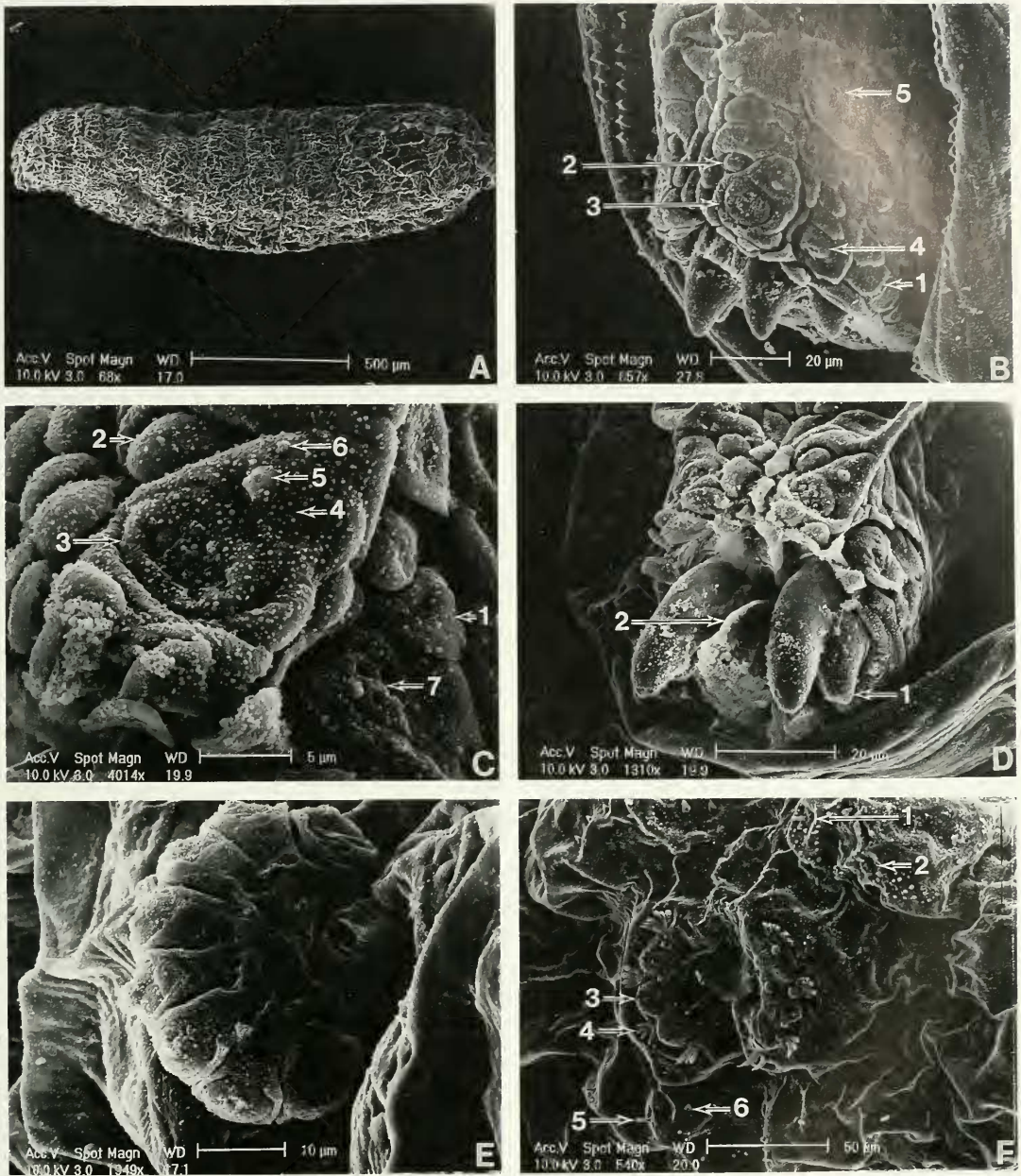
Fig. 3.   Second instar of *Trupanea wheeleri:* (A) habitus, anterior end to left; (B) gnathocephalon, anterior view, 1—serrated rugose pad, 2—dorsal sensory organ, 3—anterior sensory lobe, 4—stomal sense organ, 5—pit sensillum; (C) anterior sensory lobe, 1—serrated rugose pads, 2—dorsal sensory organ, 3—terminal sensory organ, 4—pit sensory organ, 5—lateral sensory organ, 6—supralateral sensory organ, 7—stomal sense organ; (D) gnathocephalon, anterior view, 1—mouth hook, 2—median oral lobe; (E) anterior thoracic spiracle; (F) caudal segment, 1—stelex sensillum, 2—verruciform sensillum, 3—rima, 4—interspiracular process, 5—intermediate sensory complex, stelex sensillum, 6—intermediate sensory complex, medusoid sensillum.

tersegmental lines; gnathocephalon conical (Fig. 3B); rugose pads laterad of anterior sensory lobe serrated on ventral margin (Fig. 3B-1, C-1); dorsal sensory organ a dome-shaped papilla (Fig. 3B-2, 3C-2); anterior sensory lobe (Fig. 3B-3), bears terminal sensory organ (Fig. 3C-3), pit sensory organ (Fig. 3C-4), lateral sensory organ (Fig. 3C-5), and supralateral sensory organ (Fig. 3C-6); stomal sense organ ventrolaterad of anterior sensory lobe (Fig. 3B-4, 3C-7); mouth hook bidentate (Fig. 3D-1); median oral lobe laterally flattened (Fig. 3D-2); pit sensilla circumscribe gnathocephalon (Fig. 3B-5); minute acanthae circumscribe anterior margin of prothorax; rugose pads and two rows of verruciform sensilla circumscribe prothorax; anterior thoracic spiracle bears 7–8 ovoid papillae (Fig. 3E); verruciform sensilla circumscribe mesothorax; lateral spiracular complexes not seen; caudal segment with two stelex sensilla, dorsad and ventrad of posterior spiracular plate (Fig. 3F-1); two verruciform sensilla dorsolaterad of posterior spiracular plate (Fig. 3F-2); posterior spiracular plate bears three ovoid rimae, ca. 0.018 mm in length (Fig. 3F-3), and four interspiracular processes, each with 3–6 branches, longest measuring 0.01 mm (Fig. 3F-4); intermediate sensory complex with a medusoid sensillum (Fig. 3F-5) and a stelex sensillum (Fig. 3F-6).

The second instar bears serrated rugose pads laterad of the mouth lumen similar to the second instars of *T. nigricornis* and *T. pseudovicina* (Knio et al. 1996a, Goeden and Teerink 1998). The second instars of *T. imperfecta* and *T. jonesi* lack serrated rugose pads, although the third instars of both species bear serrated rugose pads (Goeden et al. 1998a, Teerink and Goeden 1998b). In the second instar of *T. wheeleri*, the anterior spiracle bears 7–8 papillae, more than any previously studied congeneric species (Goeden and Teerink 1997b, 1998, 1999; Goeden et al. 1998a, b; Headrick and Goeden 1991; Knio et al. 1996a; Teerink and Goeden 1998, 1999). The interspiracular

processes are not as elaborately branched as those of the first instar.

Third instar: White, barrel-shaped, tapering anteriorly, rounded posteriorly, minute acanthae circumscribe intersegmental lines (Fig. 4A); gnathocephalon conical (Fig. 4B), rugose pads laterad of mouth lumen serrated on ventral margin; dorsal sensory organ a dome-shaped papilla (Fig. 4C-1); anterior sensory lobe bears terminal sensory organ (Fig. 4C-2), pit sensory organ (Fig. 4C-3), lateral sensory organ (Fig. 4C-4), and supralateral sensory organ (Fig. 4C-5); stomal sense organ ventrolaterad of anterior sensory lobe (Fig. 4C-6); mouth hooks hidden in all prepared specimens; prothorax circumscribed anteriorly with minute acanthae (Fig. 4B-1); rugose pads circumscribe prothorax posteriorad to minute acanthae (Fig. 4B-2); two rows of verruciform sensilla circumscribe prothorax posteriorad to rugose pads (Fig. 4B-3); stelex sensillum located dorsomedially (Fig. 4B-4); anterior spiracle on posterior margin of prothorax bears 3–5 rounded papillae (Fig. 4B-5, 4D); mesothorax circumscribed anteriorly with verruciform sensilla (Fig. 4B-6); metathoracic lateral spiracular complex consists of a spiracle (Fig. 4E-1), a stelex sensillum (Fig. 4E-2), and two verruciform sensilla (Fig. 4E-3); abdominal lateral spiracular complex consists of a spiracle (Fig. 4F-1) and two verruciform sensilla (Fig. 4F-2); caudal segment circumscribed by minute acanthae; two stelex sensilla, dorsad and ventrad of posterior spiracular plates (Fig. 4G-1); two verruciform sensilla dorsolaterad of posterior spiracular plates (Fig. 4G-2); posterior spiracular plate bears three ovoid rimae, ca. 0.034 mm in length (Fig. 4G-3), and four interspiracular processes, each with 3–6 branches, longest measuring 0.018 mm (Fig. 4G-4); intermediate sensory complex (Fig. 4G-5), with a medusoid sensillum (Fig. 4H-1), and a stelex sensillum (Fig. 4H-2).

The third instar bears serrated rugose pads similar to the third instars of *T. imperfecta, T. jonesi, T. nigricornis, T. pseu-*

dovicina and *T. signata* (Goeden and Teerink 1997b, 1998; Goeden et al. 1998a; Knio et al. 1996a; Teerink and Goeden 1998). Compared to the second instar, the third instar bears only 3–5 papillae on the anterior spiracle. As with the high number of papillae in the second instar, so large a reduction in the number of papillae between instars has not been reported in any other *Trupanea* species (Goeden and Teerink 1997b, 1998, 1999; Goeden et al. 1998a, b; Headrick and Goeden 1991; Knio et al. 1996a; Teerink and Goeden 1998, 1999). These atypical characteristics call the identity of the second instars examined into question, but this stage was described from 10 replicates obtained from three different host species; which would reduce the probability that the same contaminent occurred in all four samples from which second instars were obtained.

The mesothorax alone is circumscribed by verruciform sensilla, similar to *T. nigricornis* (Knio et al. 1996a); whereas both the meso- and metathorax are circumscribed by verruciform sensilla in *T. arizonensis* and *T. imperfecta* (Goeden and Teerink 1998, Teerink and Goeden 1998). The third instar lateral spiracular complex is identical to that in *T. imperfecta* (Teerink and Goeden 1998). This is the first instance in which two species of *Trupanea* have shared the same type and number of sensilla in the metathoracic and abdominal lateral spiracular complexes (Goeden and Teerink 1997b, 1998, 1999; Goeden et al. 1998a, b; Headrick and Goeden 1991; Knio et al. 1996a; Teerink and Goeden 1998, 1999). Other pairs of congeneric species in other genera are known to share the same number and type of sensilla in the lateral spiracular complexes, e.g., *Procecidochares kristineae* and *P. lisae; Aciurina idahoensis* and *A. michaeli; A. thoracica* and *A. trixa* (Goeden and Teerink 1996a, b, 1997a; Headrick and Goeden 1993; Headrick et al. 1997).

Puparium: Black, elongate-cylindrical, minute acanthae circumscribe intersegmental lines (Fig. 5A); anterior end bears the invagination scar (Fig. 5B-1) and anterior thoracic spiracles (Fig. 5B-2); caudal segment circumscribed by minute acanthae (Fig. 5C-1), two stelex sensilla. dorsad and ventrad of posterior spiracular plates (Fig. 5C-2); two verruciform sensilla dorsolaterad of posterior spiracular plates (Fig. 5C-3); posterior spiracular plate bears three ovoid rimae (Fig. 5C-4), and four interspiracular processes, each with 3–6 branches (Fig. 5C-5); intermediate sensory complex with a medusoid sensillum and a stelex sensillum. Ninety-four puparia averaged 2.53 ± 0.03 (range, 1.71–3.17) mm in length; 1.24 ± 0.02 (range, 0.85–1.72) mm in width.

DISTRIBUTION AND HOSTS

The distribution of *T. wheeleri* in North America north of Mexico as mapped by Foote et al. (1993) included Arizona, California, New Mexico, Oregon, Texas, and Utah in the western United States and a single record from near the border in adjacent western Canada.

Wasbauer (1972) and Goeden (1985, 1986, 1992) reported *T. wheeleri* from five tribes, 14 genera, and 29 species of host plants in North America. Five new rearing records for *T. wheeleri* are listed below in the manner of Goeden (1992), which along with taxonomic changes in Hickman (1993) and Goeden et al. (1998b), increase the reported host range to include seven tribes, 15 subtribes (Bremer 1994), 28 genera and 47 species. All flies were reared from ca. 1-liter samples of mature flower heads from California.

New host genera.—*Lasthenia, Machaeranthera, Psathyrotes, Senecio*

New host records.—*Erigeron aphanactis* (Gray) Greene, 3 ♂ and 1 ♀, SE of Mission Springs at 2480-m elevation, San Bernardino Nat. Forest (N section), San Bernardino Co., 17.vii.1997; *Lasthenia glabrata* Lindley, 1 ♂, San Jacinto Wildlife Area at 390 m, Lakeview, Riverside Co., 2.iv.1997; *Machaeranthera canescens* (Pursh) Gray, 1 ♂ and 1 ♀, N of Jenks Lake and S of Bar-
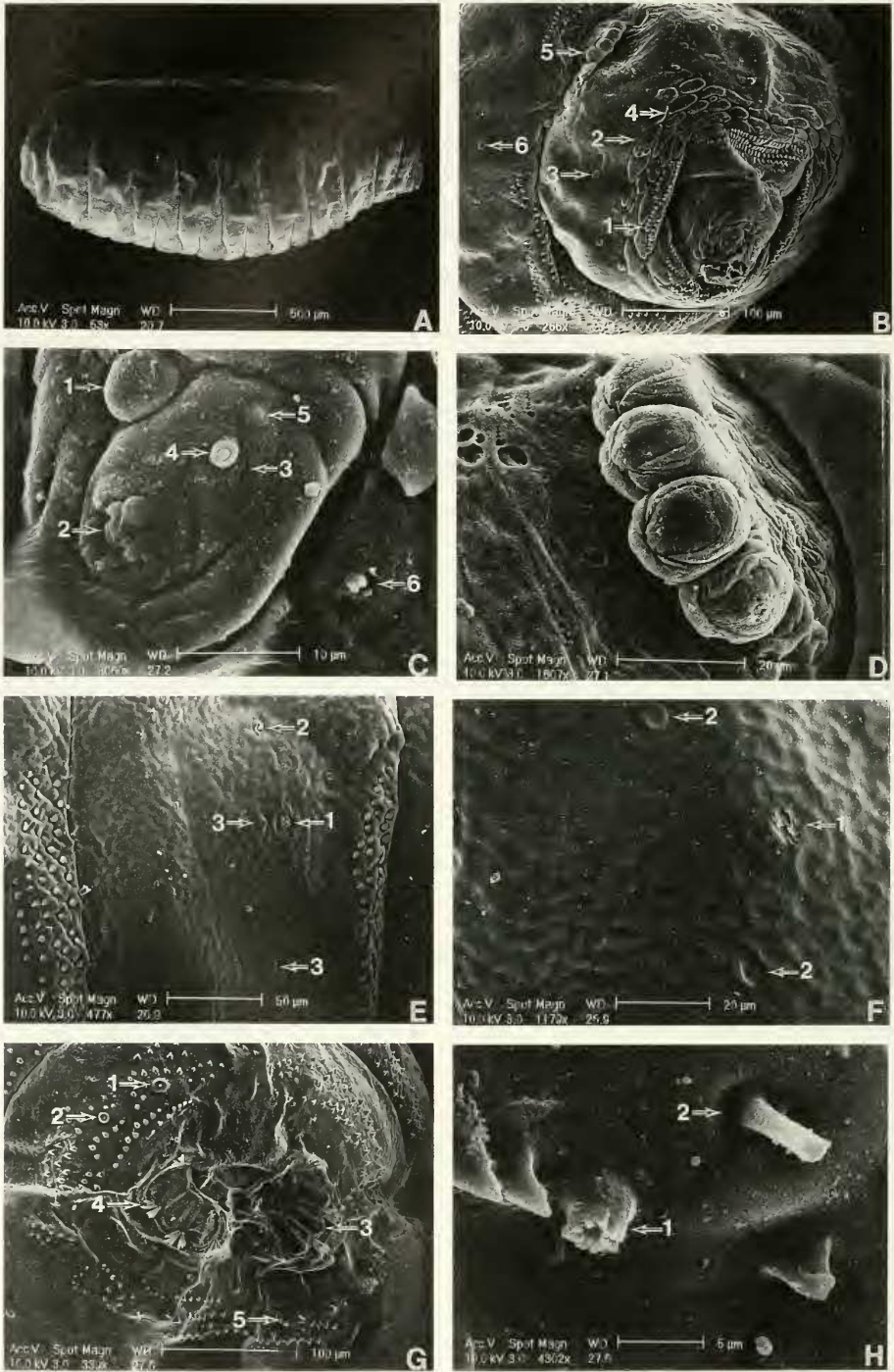
Fig. 4.   Third instar of *Trupanea wheeleri:* (A) habitus, anterior to right; (B) gnathocephalon, prothorax, anteriolateral view, 1—minute acanthae, 2—rugose pad, 3—verruciform sensillum, 4—stelex sensillum, 5—anterior thoracic spiracle, 6—verruciform sensillum; (C) anterior sensory lobe, 1—dorsal sensory organ, 2—terminal sensory organ, 3—pit sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ, 6—stomal sense organ; (D) anterior thoracic spiracle; (E) metathorax, 1—spiracle, 2—stelex sensillum, 3—verruciform sensilla; (F) first

ton Flats at 1830-m, San Bernardino Nat. Forest (N section), San Bernardino Co., 9.viii.1995; *Psathyrotes ramosissima* (Torrey) Gray, 2 ♀, Painted Canyon at 155 m, Riverside Co., 19.iii.1996; *Senecio canus* Hooker, 2 ♂ and 1 ♀, 1.6 km S of Beach Meadow at 2430 m, Sequoia Nat. Forest (N section), Tulare Co., 15.vii.1993.

All of the rearing records for the 45 reported hosts of *T. wheeleri* are from California, and all but four of these were confirmed by us or are ours or RDG's records, including nine recently reassigned from *T. actinobola* (Goeden et al. 1998b). Of the eight valid host names that Wasbauer (1972) listed, we have confirmed four. As known to date, most hosts for *T. wheeleri* belong to the tribe Astereae (26 spp.), with good representation from the Helenieae (9 spp.) and Heliantheae (4 spp.), and token representation from Eupatorieae (2 spp.), Senecioneae (2 spp.), Anthemideae (1 sp.), and Mutiseae (1 sp.) (Munz 1974, Hickman 1993, Bremer 1994). Similarly, the subtribe Solidagininae (21 spp.) is best represented, with additional representation in the subtribes Asterinae (5 spp.), Verbesininae (3 spp.), Alomiinae (2 spp.), Baeriinae (2 spp.), Chaenactidinae (2 spp.), Madiinae (2 spp.), Achilleinae (1 sp.), Gaillarediinae (1 sp.), Nassauviinae (1 sp.), Pectidinae (1 sp.), Peritylinae (1 sp.), Senecioninae (1 sp.), Tussilagininae (1 sp.) (Bremer 1994).

BIOLOGY

Trupanea wheeleri is a difficult species to study in flower heads because it usually co-occurs with other tephritids in the same host-plant species (symphagy) (Goeden 1997), including congeners, and only certain host species sampled at certain locations contained mixes of immature stages of recognizable species.

Egg.—A total of 27 eggs was recovered from preblossom flower heads of *Corethrogyne filaginifolia* (Hooker and Arnott) Nuttall, *Ericameria brachylepis* (A. Gray) H. M. Hall (=*Haplopappus propinquus* S. F. Blake) and *Hazardia* (formerly *Haplopappus*) *squarrosus* (Hooker and Arnott) Greene, for an average of 2.5 ± 0.2 (range, 1–4) eggs per flower head. All eggs were inserted pedicel-last, mostly through the phyllaries or between their appressed apices, perpendicular to or at 30° to 60° to the receptacle, and alongside or into a corolla or ovule of a floret on the periphery or at the center of a closed, immature flower head (Fig. 6A, B). Most eggs were oviposited singly (Fig. 6A, B) or side-by-side, in pairs, or rarely, in threes by single females.

Larva.—Upon eclosion, first instars tunneled into and fed mainly on corollas of florets and on ovules in preblossom flower heads. No receptacle within flower heads was pitted by first-instar feeding in a total of 10 heads of *E. brachylepis* and *H. squarrosus* (Fig. 6C).

Second instars fed mainly on ovules and florets of preblossom flower heads and soft achenes of open flower heads (Fig. 6D). Receptacles of a total of 13 flower heads of *C. filaginifolia*, *Ericameria palmeri* (Gray) Hall, and *H. squarrosus* containing second instars averaged 1.9 ± 0.3 (range, 0.9–3.7) mm in diameter and none was pitted. These flower heads contained an average of 1.7 ± 0.2 (range, 1–3) second instars that had fed upon an average of 5.3 ± 0.7 (range, 3–10) florets/ovules/achenes, or 31% (range, 9–67%) of an average total of 21 ± 4.0 (range, 8–58) florets/ovules/achenes per head.

Third instars fed on soft achenes at the centers, and less commonly to the margins, of open or postblossom flower heads (Fig.
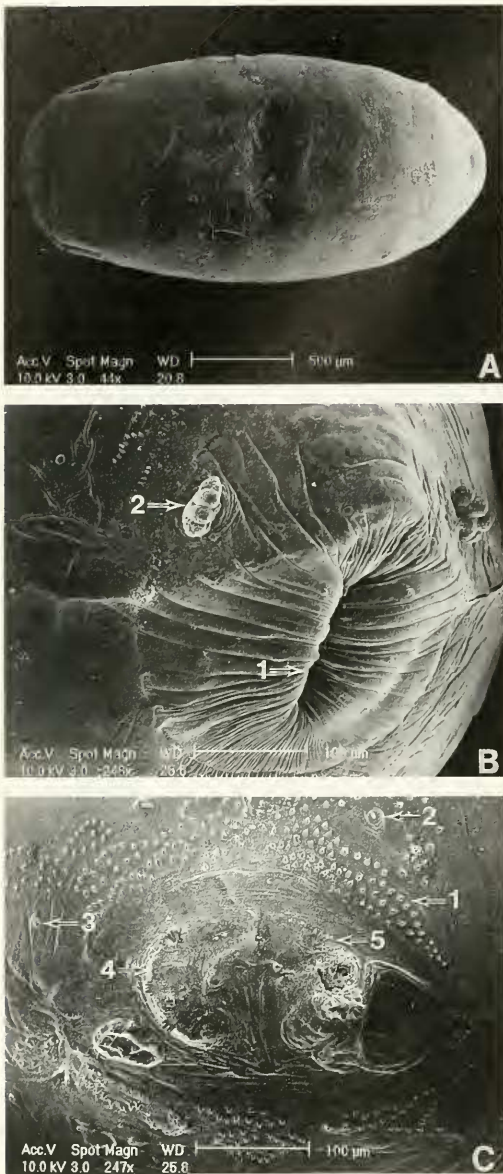
←

Fig. 5. Puparium of *Trupanea wheeleri:* (A) habitus, anterior end to left; (B) anterior end, 1—invagination scar, 2—anterior thoracic spiracle; (C) caudal segment, 1—minute acanthae, 2—stelex sensillum, 3—verruciform sensillum, 4—rima, 5—interspiracular process.

6E, F). In a total of 28 flower heads of *Acourtia* (formerly *Perezia*) *microcephala* deCandolle, *C. filaginifolia, E. palmeri,* and *H. squarrosus* averaging 1.8 ± 0.1 (range, 1.1–2.6) mm in diameter and containing an

average of 1.4 ± 0.1 (range, 1–4) third instars and 18.8 ± 1.9 (range, 6–36) achenes, an average of 6.8 ± 1.0 (range 1–23) soft achenes were damaged. Most third instars fed with their long axes oriented perpendicular to and mouthparts directed towards the receptacles, within the upper parts of the soft achenes, and well above the receptacles (Fig. 6E). Consequently, only three (11%) receptacles of flower heads that respectively contained three, two, and one third instars were pitted in the 28 flower heads examined. Upon completing feeding, the larvae oriented with their anterior ends away from the receptacles, retracted their mouthparts, and pupariated (Fig. 6F).

Pupa.—As noted with other florivorous, congeneric tephritids studied (Goeden and Teerink 1998, 1999; Goeden et al. 1998a, b), flower heads containing puparia (Fig. 6G) had the greatest amount of damage that the seed-feeding larvae of *T. wheeleri* caused within flower heads sampled. The receptacles of 90 infested, blossom and postblossom flower heads of *A. microcephala, C. filaginifolia, E. palmeri,* and *H. squarrosus* containing puparia averaged 1.7 ± 0.1 (range, 0.9–2.9) mm in diameter and bore an average of 15.2 ± 1.1 (7–32) soft achenes, of which an average of 6.9 ± 0.6 (range, 1–16) soft achenes or 45% (range, 19–100%) were damaged. About half of the receptacles were pitted and about half of the puparia were found next to the phyllaries at the margins of flower heads; the remaining flower heads contained puparia at or near their centers (Fig. 6G). All puparia had their anterior ends facing away from the receptacles, and their long axes were perpendicular to the receptacles (Fig. 6G).

Adult.—Adults emerged from mature flower heads, and were long-lived under insectary conditions, as 20 unmated males (Fig. 6H, I) averaged 91 ± 11 (range, 32–230) days, and 23 virgin females (Fig. 6H) averaged 68 ± 8 (range, 21–181) days. Like *T. actinobola, T. arizonensis, T. jonesi,* and *T. pseudovicina* (Goeden and Teerink 1998, 1999; Goeden et al. 1998a, b), these flies
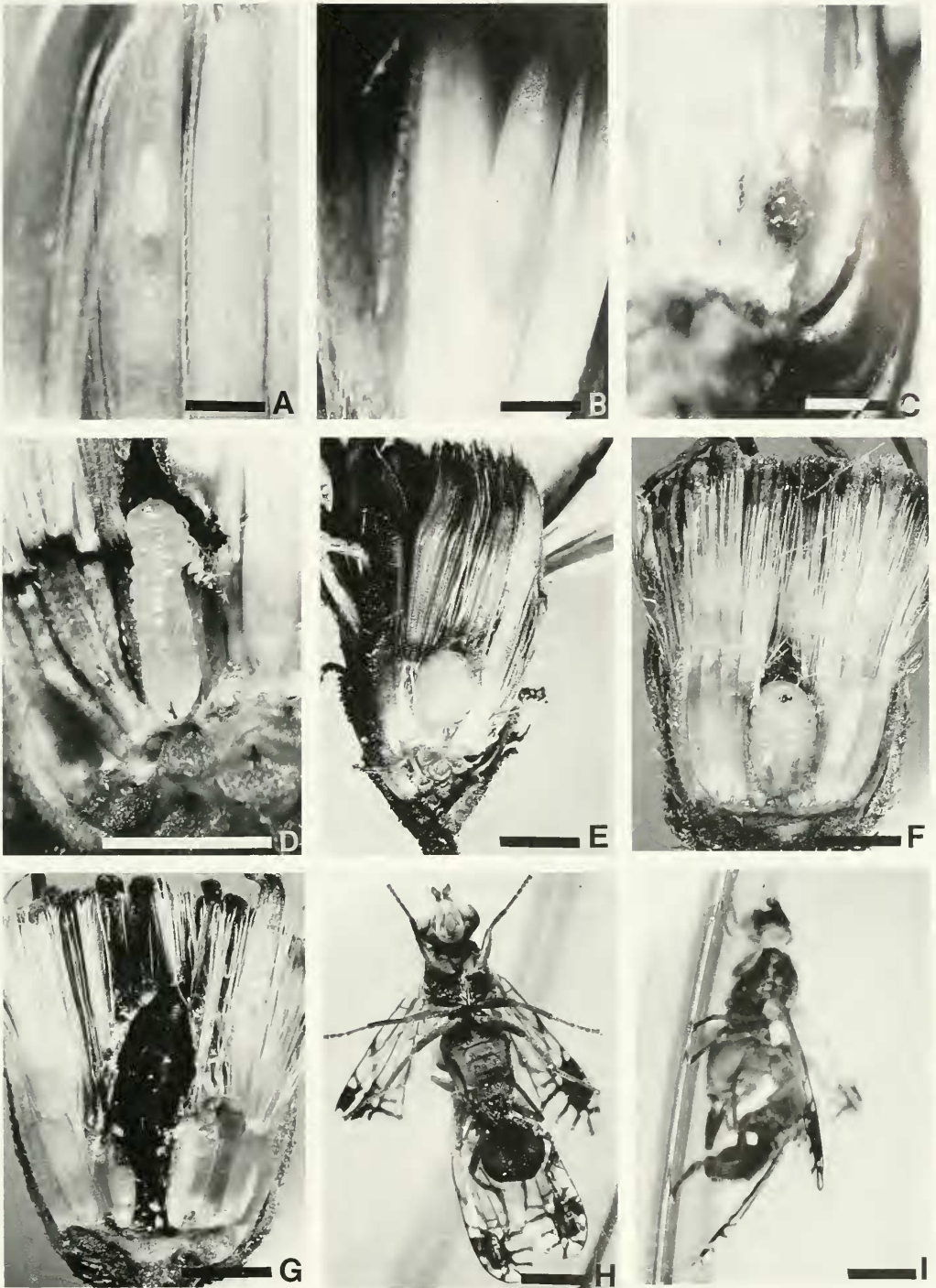
Fig. 6.   Life stages of *Trupanea wheeleri:* (A) egg inserted in corolla of floret of *Machaeranthera canescens;* (B) egg inserted in corolla of floret of *Corethrogyne filaginifolia;* (C) first instar in ovules in flower head of *M. canescens;* (D) second instar tunneling in ovules in flower head of *C. filaginifolia;* (E) third instar in center of open flower head of *C. filaginifolia;* (F) late third instar in center of open flower head of *Erigeron foliosus* Nuttall; (G) puparium in flower head of *Erigeron foliosus;* (H) mating pair, ventral view; (I) mating pair, side view. Lines = 1 mm.

are among the longer average and maximum adult longevities that we have recorded for native species of nonfrugivorous Tephritidae from southern California. Such lengthy longevities are consistent with the aggregative type of life cycle ascribed below to this tephritid.

The premating and mating behaviors of *T. wheeleri* were briefly studied in the laboratory; however, the petri dish arenas found to be so useful with many other Tephritinae species (Headrick and Goeden 1994), but unsatisfactory with most *Trupanea,* facilitated only two matings of 5 and 7 minutes duration each observed between 14:00 and 15:00 h PDST (Fig. 6H, I). See Headrick and Goeden (1994), Knio et al. (1996b), Goeden et al. (1998a, b) for descriptions of premating and mating behaviors of congeneric California species.

Seasonal history.—The life cycle of *T. wheeleri* in southern California follows an aggregative pattern in which the long-lived adults in reproductive diapause overwinter and aggregate to mate on preblossom host plants in the spring (March–April) (Headrick and Goeden 1994). They reproduce first in the Colorado Desert, then in the higher-elevation Mojave Desert, interior valleys, and coastal areas (Headrick and Goeden 1994). Like *T. jonesi* (Goeden et al. 1998a) and *T. nigricornis* (Knio et al. 1996b), reproduction by subsequent generations of these multivoltine tephritids continue thereafter throughout the spring, summer, and fall on a wide range of alternate host plants, as flowering of Asteraceae continues at ever higher elevations and more northerly latitudes in California.

Natural enemies.—Seven species of chalcidoid Hymenoptera were reared from individual puparia and mature flower heads bearing puparia of *T. wheeleri* as solitary, primary, larval-pupal endoparasitoids: *Eurytoma* n. sp.? (Eurytomidae), *Eurytoma obtusiventris* Gahan (Eurytomidae), *Eurytoma veronia* Bugbee (Eurytomidae), *Eupelmus* sp. (Eupelmidae), *Mesopolobus* sp. (Pter-

omalidae), *Pteromalus* sp. (Pteromalidae), *Torymus* sp. (Torymidae).

Literature Cited

Bremer, K. 1994. Asteraceae Cladistics & Classification. Timber Press, Inc. Portland, Oregon.

Cavender, G. L. and R. D. Goeden. 1982. Life history of *Trupanea bisetosa* (Diptera: Tephritidae) on wild sunflower in southern California. Annals of the Entomological Society of America 75: 400–406.

Curran, C. H. 1932. New species of Trypanidae, with a key to the North American genera. American Museum Novitates 556: 1–19.

Foote, R. H. 1960. A revision of the genus *Trupanea* in America north of Mexico. U.S. Department of Agriculture Technical Bulletin 1214. 29 p.

Foote, R. H. and F. L. Blanc. 1963. The fruit flies or Tephritidae of California. Bulletin of the California Insect Survey 7, 117 p.

Foote, R. H., F. L. Blanc, and A. L. Norrbom. 1993. Handbook of the Fruit Flies (Diptera: Tephritidae) of America North of Mexico. Cornell University Press, Ithaca, New York.

Goeden, R. D. 1985. Host-plant relations of *Trupanea* spp. (Diptera: Tephritidae) in southern California. Proceedings of the Entomological Society of Washington 87: 564–571.

———. 1986. New records of Tephritidae (Diptera) from Santa Cruz Island, California. Pan-Pacific Entomologist 62: 326–328.

———. 1987. Life history of *Trupanea conjuncta* (Adams) on *Trixis californica* Kellogg in southern California (Diptera: Tephritidae). Pan-Pacific Entomologist 63: 284–291.

———. 1988. Life history of *Trupanea imperfecta* (Coquillett) on *Bebbia juncea* (Bentham) Greene in the Colorado Desert of southern California

(Diptera: Tephritidae). Pan-Pacific Entomologist 64: 345–351.

———. 1992. Analysis of known and new host records for *Trupanea* from California (Diptera: Tephritidae). Proceedings of the Entomological Society of Washington 94: 107–118.

———. 1997. Symphagy among florivorous fruit flies (Diptera: Tephritidae) in southern California. Chapter 3 *In:* K. Dettner, G. Bauer, and W. Völkl (eds.). Vertical Food Web Interactions: Evolutionary Patterns and Driving Forces. Ecological Studies 130: 39–52.

Goeden, R. D. and J. A. Teerink. 1996a. Life histories and descriptions of adults and immature stages of two cryptic species, *Aciurina ferruginea* (Doane) and *A. michaeli*, new species (Diptera: Tephritidae), on *Chrysothamnus viscidiflorus* (Hooker) Nuttall in southern California. Proceedings of the Entomological Society of Washington 98: 415–438.

———. 1996b. Life history and descriptions of adults and immature stages of *Aciurina idahoensis* Steyskal (Diptera: Tephritidae) on *Chrysothamnus viscidiflorus* (Hooker) Nuttall in southern California. Proceedings of the Entomological Society of Washington 98: 681–694.

———. 1997a. Notes on life histories and descriptions of adults and immature stages of *Procecidochares kristineae* and *P. lisae* new species (Diptera: Tephritidae) on *Ambrosia* spp. in southern California. Proceedings of the Entomological Society of Washington 99: 67–88.

———. 1997b. Life history and description of immature stages of *Trupanea signata* Foote (Diptera: Tephritidae) on *Gnaphalium luteo-album* L. in southern California. Proceedings of the Entomological Society of Washington 99: 747–754.

———. 1998. Life history and description of immature stages of *Trupanea pseudovicinia* Hering (Diptera: Tephritidae) on *Porophyllum gracile* Bentham (Asteraceae) in southern California. Proceedings of the Entomological Society of Washington 100: 361–372.

———. 1999. Life history and description of immature stages of *Trupanea arizonensis* Hering (Diptera: Tephritidae) on *Trixis californica* Kellog var. californica (Asteraceae) in southern California. Proceedings of the Entomological Society of Washington 101: 75–85.

Goeden, R. D., J. A. Teerink, and D. H. Headrick. 1998a. Life history and description of immature stages of *Trupanea jonesi* Curran (Diptera: Tephritidae) on native Asteraceae in southern California. Proceedings of the Entomological Society of Washington 100: 126–140.

———. 1998b. Life history and description of immature stages of *Trupanea actinobola* (Loew) (Diptera: Tephritidae) on *Acamptopappus sphaerocephalus* Harvey and Gray Gray (Asteraceae) in southern California. Proceedings of the Entomological Society of Washington 100: 674–688.

Headrick, D. H. and R. D. Goeden. 1991. Life history of *Trupanea californica* Malloch (Diptera: Tephritidae) on *Gnaphalium* spp. in southern California. Proceedings of the Entomological Society of Washington 93: 559–570.

———. 1993. Life history and description of immature stages of *Aciurina thoracica* (Diptera: Tephritidae) on *Baccharis sarothroides* in southern California. Annals of the Entomological Society of America 86: 68–79.

———. 1994. Reproductive behavior of California fruit flies and the classification and evolution of Tephritidae (Diptera) mating systems. Studia Dipterologica 1(2): 194–252.

Headrick, D. H., R. D. Goeden, and J. A. Teerink. 1997. Taxonomy of *Aciurina trixa* Curran (Diptera: Tephritidae) and its life history on *Chrysothamnus nauseosus* (Pallas) Britton in southern California; with notes on *A. bigeloviae* (Cockerell). Proceedings of the Entomological Society of Washington 99: 415–428.

Hickman, J. C. (ed.) 1993. The Jepson Manual. University of California Press. Berkeley and Los Angeles.

Knio, K. M., R. D. Goeden, and D. H. Headrick. 1996a. Descriptions of immature stages of *Trupanea nigricornis* and *T. bisetosa* (Diptera: Tephritidae) from southern California. Annals of the Entomological Society of America 89: 1–11.

———. 1996b. Comparative biologies of the cryptic, sympatric species, *Trupanea nigricornis* and *T. bisetosa* (Diptera: Tephritidae) in southern California. Annals of the Entomological Society of America 89: 252–260.

Munz, P. A. 1974. A Flora of Southern California. University of California Press, Berkeley and Los Angeles.

Teerink, J. A. and R. D. Goeden. 1998. Description of the immature stages of *Trupanea conjuncta* (Adams). Proceedings of the Entomological Society of Washington 100: 431–438.

———. 1999. Description of the immature stages of *Trupanea imperfecta* (Coquillett). Proceedings of the Entomological Society of Washington 101:

Wasbauer, M. W. 1972. An annotated host catalog of the fruit flies of America north of Mexico (Diptera: Tephritidae). California Department of Agriculture, Bureau of Entomology Occasional Papers 19, 172 pp.